



structure and function, but these have been largely unexplored.

The conceptual framework for understanding ecosystem responses to precipitation variability originates in research on arid ecosystems showing that ecosystem responses to rainfall patterns depend on the temporal separation of rainfall pulses and the extent of inactivity between pulses (Noy-Meir, 1973). Soils play a crucial role by capturing discontinuous inputs of precipitation, and making it available for plant and microbial function in amounts and durations determined, in part, by soil physical properties, vegetation, and disturbance (Reynolds et al., 2004; Rodriguez-Iturbe and Porporato, 2004). Ecosystem responses to altered precipitation variability may differ among wet or dry systems or years, depending on how often thresholds of too little or too much soil moisture are exceeded (Knapp et al., 2008). For example, Heisler-White et al. (2009) found that increased growing season rainfall variability resulted in increased net primary productivity in semiarid grasslands, but decreased it in more



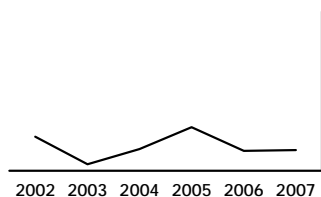
stored as 30 min averages on data loggers. We used the daily average

each May through October. Winter  $J_{\text{CO}_2}$  was measured on 7–9 snow-free dates during November through March in 2005/2006 and 2006/2007.  $J_{\text{CO}_2}$  was measured at two permanently installed PVC collars (8 cm diam, 1.7 cm height inserted to 1.2 cm) at four locations per plot during 1998–2002, and at two collars per subplot from 2003–2007. Data from 1998–2001 were reported in Harper et al. (2005).  $J_{\text{CO}_2}$  rates were estimated from the linear rise in  $\text{CO}_2$  concentration over 1 to 3 min.

## 2.5 Data analysis

Intra-annual rainfall variability was quantified by computing the coefficient of variation (CV) from the daily rainfall amounts applied to the RaMPs during the growing season (1 May–30 September). Mean growing season

$J_{\text{CO}_2}$  was quantified. Variability during growing season in  $J_{\text{CO}_2}$  was quantified



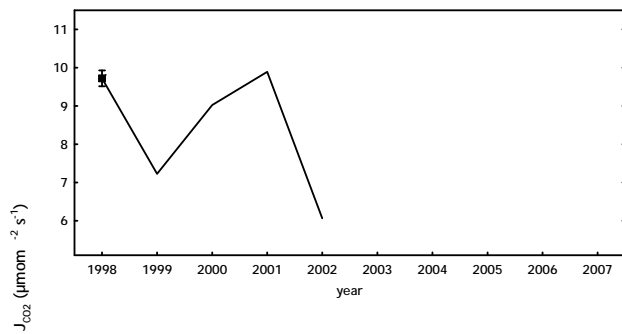
**Fig. 1.** Annual rainfall inputs and soil moisture means and variability in the RaMPs experiment during the rainfall pattern  $\times$  quantity treatments (Phase I, 1998–2001) and the rainfall pattern  $\times$  warming treatments (Phase II, 2003–2007). **(A)** Total growing season rainfall. **(B)** Probability density functions of individual rainfall event size (100 % treatments) and dry interval length. **(C)**











**Fig. 7.** Soil  $\text{CO}_2$  efflux ( $J_{\text{CO}_2}$ ) by rainfall and warming treatments. (A) Mean growing season  $J_{\text{CO}_2}$  by year, symbols as in Fig. 1. Growing season mean  $J_{\text{CO}_2}$  during (B) Phase I and (C) Phase II. (D) Winter  $J_{\text{CO}_2}$  by rainfall pattern and warming during 2006–2007. Note that scaling for (D) differs from that for (B–C). Error bars denote 1 SE of the mean.

Interannual variability in  $A_{\text{CO}_2}$  of the grasses was of comparable magnitude to that of total ANPP. We expected interannual variability to have a smaller effect on  $A_{\text{CO}_2}$  relative to that of intra-annual rainfall variability, because  $A_{\text{CO}_2}$  in these grasses decreases strongly with soil moisture depletion, and recovery is often slow when soil moisture is restored, especially after extended drought (Knapp, 1985; Heckathorn et al., 1997). Leaf level photosynthesis has been associated with long-term (1998–2007) success (McAllister et al., 1998), and the ability to track soil moisture variability is crucial to the success (Swemmer et al., 2006; Nippert et al., 2006a). The finding that  $A_{\text{CO}_2}$  was strongly correlated with  $J_{\text{CO}_2}$  (Table 1) suggests that on average,  $A_{\text{CO}_2}$  was strongly coupled to interannual climate variation and associated interannual differences in soil water supply.

High responsiveness (grass) (9.963 Td(A)) (7.572 Tf 7.273 -1.498 Td[(CO)]) (5.978 Tf 1

Increased intra-annual rainfall variability significantly affected most ecosystem processes when compared to an equal amount of rainfall at ambient variability. However, the effects of interannual variation for soil moisture and most ecosystem processes were considerably larger than the effect of increased intra-annual variability (Fig. 9a inset) and most ecosystem processes. Increased rainfall variability reduced plant growth and leaf and soil CO<sub>2</sub>





*Acknowledgements.*



